

PLANTS AS INDICATORS OF LEAFCUTTER BEE (HYMENOPTERA: MEGACHILIDAE) NEST HABITAT IN COASTAL DUNES

DAVID M. GORDON

Division of Mathematics and Sciences, Kentucky State University,
Frankfort, Kentucky 40601

Abstract.—To conserve native plants, pollinators and their nesting habitats must also be protected. Indicator plants for nesting sites of the native leafcutter bee *Megachile wheeleri* Mitchell were characterized within a Northern California coastal dunes preserve. Nesting was restricted to the *Poa-Lathyrus* plant community. Significant positive associations were detected between bee nests and *Aira praecox* L., *A. caryophyllea* L., *Solidago spathulata* DC., *Juncus lesueurii* Bolander, and mosses; negative associations with *Carex obnupta* L. Bailey and *Lathyrus littoralis* (Nuttall) Endlicher. Nest density and total plant cover were not significantly correlated. Nests were generally not constructed near the bee's host plants. Most nesting occurred in a zone transitional between mesic lowlands and xeric higher elevations. Natural successional change was increasing nesting habitat, but climax shore pine-spruce forest should eventually eliminate nesting habitat in the long term if succession is not disturbed. The introduced plants *Lupinus arboreus* Sims and *Ammophila arenaria* L. may eliminate nest habitat, but *Aira praecox* L. and *A. caryophyllea* L. may enhance it. Other bee and wasp species were present in samples but no significant associations with plants were detected because densities were so low. Very large sample sizes will be required to determine significant associations for those species. *M. wheeleri* nests ranged from dense aggregations to scattered individual nests. Other bee and wasp species also nested within *M. wheeleri* nest aggregations, including the sphecoid wasp *Bembix americana comata* J. Parker, which normally nests in barren sand. Native plant restoration activities may benefit from restoration of native pollinators.

Key Words.—Hymenoptera, Megachilidae, solitary bee conservation, nest habitat, plant community, pollination.

Bees and flowering plants have evolved close associations (reviewed by Crepet 1983), and the importance of bees as pollinators has long been known (reviewed in Kevan & Baker 1983, O'Toole, 1993, Proctor, Yeo & Lack 1996). There is a growing awareness that in order to preserve native plants, it is also important to preserve native bees (Tepedino 1979, Kevan 1986, Roubik 1989, Bawa 1990, Thorp 1990, Osborne et al. 1991, Neff & Simpson 1993, O'Toole 1993, Vinson et al. 1993, Buchmann & Nabhan 1996, Kearns et al. 1998) and that the loss of native bee populations may threaten the survival of endangered plants (Loope et al. 1988, Tepedino et al. 1990, Cole et al. 1992). To conserve native bee populations it is important to protect their nests (Hurd & Michener 1955, Thorp 1990, Gordon 1992a, Vinson et al. 1993) and this will require identification of both potential and actual nesting sites.

The Lanphere-Christensen Dunes Preserve (L-CDP) includes the least disturbed coastal dune system in the Northern Pacific Border Region (Sweet 1981). Previous work on the preserve's bee fauna (Gordon 1984, Thorp & Gordon 1992) suggested that nesting habitats used by a ground-nesting leafcutter bee contained distinctive plant associations. The objective of this study was to identify the plant species that could be used to characterize nesting habitats of *Megachile wheeleri* Mitchell (Megachilidae) within the preserve.

MATERIALS AND METHODS

Study Organism.—The leafcutter bee *M. wheeleri* is one of the most abundant native bees in the L-CDP fauna (Gordon 1984, 1992a). Within the study site, its primary pollen and nectar sources are *Achillea borealis* Bongard ssp. *arenicola* (A. A. Heller) Keck, *Erigeron glaucus* Belenden. and *Solidago spathulata* DC., although *Hypochoeris radicata* L. is occasionally visited by both sexes, and males take nectar from *Polygonum paronychia* Chamisso & Schlechtendahl. It is a ground-nesting solitary bee that generally constructs a single distinctive brood cell from leaf pieces in burrows 1 to 7 cm deep (Gordon 1984, 1992a). Dense nest aggregations are common, but individual nests can also be found scattered throughout the dunes. A single generation is produced each year, with adults beginning to emerge in June and nesting continuing into mid-September. Prepupae overwinter in cocoons and pupate in early spring. *Megachile perihirta* Cockerell has been collected in the L-CDP, but is very rare and uses different plant species for leaf sources (Gordon 1984) which could be easily distinguished from *Solidago* leaves. Several other species of bees and wasps were known to nest within *M. wheeleri* nest aggregation sites.

Study Site.—The study was conducted within the original 76 hectares of the L-CDP on the North Spit of Humboldt Bay near Arcata, California during the summers of 1988 and 1989. Approximately 1 km wide, the spit is bounded on the west by the Pacific Ocean and on the east by the Mad River Slough. An older dunes system (Cooper 1967) bordering the slough has been stabilized by a mature shore pine and Sitka spruce forest with thick underbrush. Younger dunes between the forest and the ocean have been partially stabilized by vegetation, but also contain lowlands with younger shore pine forests and expanses of barren moving sand.

The coastal dune system is a dynamic mosaic of vegetational communities and sand formations which cycle over time (Barbour & Johnson 1988, Carter 1988, Brown & McLachlan 1990). Adjacent to the beach, a ridge of foredunes rising to 8 m elevation has been semi-stabilized by vegetation. Behind the foredunes is the deflation plain, a low elevation zone that has been eroded by spring winds. During the rainy season, fresh water ponds often form for 3–6 months in these lowlands. Within the span of 30 years, succession in the deflation plain can proceed from barren deflation plain through rushes, sedges, and willows to a dense forest of shore pine and brush (Wiedemann 1984). Farther inland, semi-stabilized dune ridges with sparse to complete plant cover range from 0.5–24 m elevation, and barren moving dunes range up to 17 m.

The vascular plant flora contains 161 species, 46 (29%) of which are introduced (Barker 1976). Dense stands of two introduced species, bush lupine (*Lupinus arboreus* Sims) and European beach grass (*Ammophila arenaria* [L.] Link), have replaced much native vegetation in dunes adjacent to the study area (Wiedemann 1984, Miller 1988, Gordon 1992a).

Descriptions and photographs of the study site are provided by Sweet (1981), Wiedemann (1984), Barbour et al. (1985), Barbour & Johnson (1988), Gordon (1992a, b). The dynamics and vegetation of coastal dunes are described by Cooper (1967), Ranwell (1972), Wiedemann et al. (1974), Chapman (1976), Carter (1988), Brown & McLachlan (1990), and Nordstrom & Psuty (1990).

Nest Distribution.—Thirteen strata were defined based on my own experience (Gordon, 1984) and published plant associations (Wiedemann et al. 1974, Barbour and Johnson 1977, Wiedemann 1984). The *Poa-Lathyrus* community (Barbour and Johnson 1977) was subdivided because I suspected that elevation or proximity to the ocean might influence nesting. The Transitional Dunes stratum was defined because dense nest aggregations were known to occur in this zone where the Lowlands intergrade with Foredunes or Inland Dunes (Gordon 1984). Characteristics of strata are provided in Table 1. Photographs of habitats which contained bee nests are provided in Gordon 1992b.

Belt transects 33 m wide perpendicular to the prevailing topographic pattern of ridges and troughs were laid out on a map and six were randomly selected for sampling. Within strata, 20 sample units were randomly chosen in one of eight compass directions and distances apart (1 to 10 m). After estimating the proportion of surface covered by each plant species, sample units were excavated and the number of nest cells of bees and wasps were counted (Table 2). Because of the need to minimize the disturbance created by excavating within the preserve, sample unit (SU) size was restricted to 0.1 sq. m (31.6×31.6 cm). This SU was large enough to contain up to 42 bee nests and 6 plant species that were in the immediate vicinity of nests, and was adequate for determining associations (Ludwig & Reynolds 1988, Kenkel et al. 1989). If a SU contained an endangered plant, another SU was chosen. Because nest sites were expected to be relatively rare, a large number of samples were taken within each stratum ($n = 120$: 20 per stratum in 6 transects). One stratum, an old pasture, was present in only one transect.

Trap nests (Krombein 1967) were placed in five active nesting sites through one nesting season to verify that *M. wheeleri* did not nest in pre-existing cavities. Forty four trap nests with 7.9 mm diameter holes and 189 trap nests with 11.1 mm holes, were placed on 12 Jul 1989 and recovered on 21 May 1990. Individual trap nests were hung one m above ground in trees, placed on the ground surface, and buried at an angle similar to nests with the hole exposed at the surface.

Species Identification.—Vascular plants were identified to genus or species based on the preserve flora (Barker 1976) and nomenclature adjusted to conform with Hickman (1993). Species of lichens and mosses were not distinguished. Specimens of insects and cocoons were deposited in the Bohart Museum of Entomology at the University of California, Davis and in the L-CDP Insect Collection at Humboldt State University, Arcata, California. Bee and wasp species identifications were based on specimens from the preserve insect collection which had been identified by authorities (Gordon 1984).

Associations.—Indicator species were determined from significant associations by pairwise contingency tests of all species present in SUs (Tables 2 and 3). Association indices were calculated for species pairs with significant Yates' chi-square values, except for those with expected frequencies < 1 or with two cells containing < 5 (Ludwig & Reynolds 1988). A variance test for multispecies association (Schluter 1984, Ludwig & Reynolds 1988) was applied to all species displaying a significant positive or negative associations (Schluter 1984) with *M. wheeleri* based on the pairwise contingency tests (Table 3). The correlation between the log of the number of *M. wheeleri* nests and arcsine transformed proportion of total plant cover was tested.

Table 1. Definitions of strata used for nest distribution sampling, including elevation, description, characteristic plant species, and cross-references to published community types^{a, b, c}.

1	Old Forest, High Understory: (3–20 m) Closed canopy; dense underbrush 2–3 m high. <i>Pinus contorta</i> , <i>Picea sitchensis</i> , <i>Vaccinium ovatum</i> .
3	Old Forest, Low Understory: (3–20 m) Closed canopy forest. <i>Pinus contorta</i> , <i>Picea sitchensis</i> , <i>Gaultheria shallon</i> , <i>Arctostaphylos uva-ursi</i> , lichens.
3	Old Pasture: (10 m) Portion of Old Forest that had been grazed in past. Introduced forage grasses, <i>Solidago spathulata</i> , <i>Lupinus arboreus</i> , <i>Arctostaphylos uva-ursi</i> , <i>Gaultheria shallon</i> , <i>Pinus contorta</i> , <i>Picea sitchensis</i> , <i>Vaccinium ovatum</i> .
4	Inland Dunes: (0.5–24 m) Xeric semi-stabilized dunes more than 100 m from strand. <i>Poa douglassi</i> , <i>Lathyrus littoralis</i> , <i>Solidago spathulata</i> , <i>Erigeron glaucus</i> , <i>Achillea borealis</i> , <i>Eriogonum latifolium</i> , <i>Franseria chamissonis</i> . <i>Poa-Lathyrus</i> type ^a <i>Poa/Lathyrus</i> and <i>Festuca rubra/Solidago spathulata</i> types ^b
5	Transitional Dunes: (0.1–1 m): Transition zone between Lowlands and Inland Dunes or Foredunes. <i>Juncus lesueurii</i> , <i>Solidago spathulata</i> , <i>Fragaria chiloensis</i> , <i>Aira preacox</i> , <i>A. caryophylla</i> . Lowlands of <i>Poa-Lathyrus</i> type ^{a,b} transitional into <i>Salix-Rubus</i> ^a and <i>Carex obnupta/Potentilla pacifica</i> ^b types. Similar to “Dry Meadow” and “Wet Meadow” deflation plain communities ^c .
6	Lowlands: (–0.5 to +0.5 m.) Hydric to mesic barren to early successional vegetation in deflation plain. Submerged by fresh water ponds 3–6 months. <i>Carex obnupta</i> , <i>Juncus lesueurii</i> , <i>J. falcatus</i> . <i>Salix-Rubus</i> ^a ; and <i>Carex obnupta/Potentilla pacifica</i> ^b types.
7	Young Forest: (–0.3 to + 1 m) Young forest within deflation plain ranging from open to closed canopy. Usually a dense mat of surface vegetation and detritus. <i>Pinus contorta</i> , <i>Salix</i> spp., <i>Juncus lesueurii</i> , mosses, <i>Carex obnupta</i> . <i>Salix-Rubus</i> ^a <i>Pinus contorta/Carex obnupta</i> and <i>Picea—Pinus/Salix</i> types. ^b
8	Moving Dune, Inland: (0.3–20 m) Barren blow sand including parabola dunes and slipfaces. More than 100 m from strand.
9	Foredunes: (0.5–5 m) Same characteristics as Inland Dunes but ranging from beach grass zone to less than 100 m. from strand.
10	Blowout Channel: (0.5–5 m) Mostly barren wind erosion channels with shallow to steeply sloped walls of aggregated sand.
11	Beach Grass Zone: (1–5 m) Grass-dominated zone above strand less than 20 m wide. <i>Elymus mollis</i> , <i>Abronia latifolia</i> , <i>Cakile maritima</i> . <i>Elymus-Cakile</i> type ^a
12	Moving Dune, Foredune: (1–5 m) Barren blowsand including moving dunes and slipfaces. Less than 100 m from strand.
13	Strand: (0–1 m) Intertidal zone, annually inundated by ocean, mostly undisturbed during summer, sparsely vegetated above summer high tide line. <i>Cakile maritima</i> , <i>Elymus mollis</i> , <i>Abronia latifolia</i> .

^a Barbour and Johnson 1977.

^b Wiedemann 1984.

^c Wiedemann, et al. 1974.

Preferences among strata were evaluated by contingency table comparisons of numbers of SUs occupied per stratum, and by comparing numbers of nests in each SU by stratum with the Mann-Whitney *U*-test. The Old Pasture was not included in tests because of the smaller sample size and lack of replication.

Correspondence analysis (Gauch 1982, Greenacre 1984, Weller & Romney 1990) was used to describe the relationships among species and SUs in the four

strata which contained *M. wheeleri* nests. To compare similar units, counts of nest cells were converted to proportions of total numbers for each species (Gauch 1982, Weller & Romney 1990). Arcsine transformed proportions were analyzed with a computer program developed by Orloci & Kenkel (1985). The Old Pasture stratum was not included because it was a unique, unreplicated habitat which had been severely disturbed by cattle grazing and contained only six nests. This outlier severely compressed the relationships of the four strata (Gauch 1982) that were of primary interest. Stability of the ordinations (Greenacre 1984) was tested by running a series of analyses using different forms of the data set (Gauch 1982). The results from analyzing all SU ($n = 464$, Table 2) are presented in Fig. 1. Sixteen sample units were eliminated from the final analysis because they contained zero records for all species. Six plant species were eliminated before the final analysis because they occurred in only one (*Anaphalis margaritacea* (L.) Bentham & Hooker, *Epilobium watsonii* (Barbey) P. Hoch & Raven, *Plantago lanceolata* L., *Rubus ursinus* Chamisso & Schlechtendahl) or two SUs (*Rumex acetosella* L., *Trifolium wormskioldii* Lehmann), and one outlier was eliminated (*Ambrosia chamissonis* (Lessing) E. Greene) because it compressed the ordination of the remaining 38 species (Gauch 1982).

RESULTS

Nest Distribution.—Trap nesting recovered a total of fourteen *M. wheeleri* brood cells from trap nests: three that were buried and seven placed on the surface. All the cells were constructed from goldenrod leaves. Construction of three brood cells did not progress past leaf collection, and one trap nest contained only pollen without leaves. Only one bee in the ten completed brood cells survived, all others died in egg or early larval stages. None of the trap nests hung in trees were occupied.

Brood cells of three bee and two sphecid wasp species were recovered from five strata (Tables 2 and 3). Three strata contained 97% of the 203 *M. wheeleri* nests: Inland Dunes, Transitional Dunes, and Foredunes (Table 4). These three strata constitute an assemblage of annual and perennial herbs classified as the "Poa-Lathyrus" community type by Barbour & Johnson (1988), including the "established dune," "dune slope," and "stabilized ridge" habitats.

Thirty seven of the 360 sample units within these three strata contained *M. wheeleri* nest cells (Tables 2 and 5). One *M. wheeleri* brood cell was found in the Lowlands and six in the Old Pasture. Sixty-five percent of the Lowlands SUs had 100% cover, 40% in the Old Pasture, and 15% or less in the other three strata. Only eight of 480 SUs were completely covered by a single plant species. Within the 4 strata, the maximum number of plant species in a SU was six (Mode = 3, mean = 2.77 ± 0.13 SE). Two SUs within Old Pasture contained nests. Both had 33% cover and contained *S. spathulata* and introduced forage grasses up to 0.5 m tall.

Comparing the Inland Dunes and the Foredunes, there was no significant difference in total numbers of SUs containing nests. However, the Transitional Dunes contained significantly less SUs with nests than the Foredunes and Inland Dunes (Table 5). There was no significant difference in the numbers of nests per SU in the Foredunes ($84/120 = 0.70$) and Inland Dunes ($38/120 = 0.32$ nest per SU) ($U = 7149.5$, $P = 0.833$, $n_1 = 120$, $n_2 = 120$), but the Transitional Dunes (74/

Table 2. Species used in correspondence analysis and their constancy within habitats (percent of sample units containing each species). Species relationships illustrated in Fig. 1 are identified by species numbers from this table.

#	Species	Percent of sample units							
		A Pasture	B Lowland	C Transition	D Foredune	E Inland	ABCDE	BCDE	CDE
Insects									
1	<i>Ammophila azteca</i> Cameron ^a	0	1.7	12.0	0.8	1.7	3.8	4.0	4.7
2	<i>Anthidium palliventre</i> Cresson ^b	0	0.8	0.8	0	5.8	1.8	1.9	2.2
3	<i>Bembix americana comata</i> J. Parker ^a	10.0	2.5	4.2	0	3.3	2.8	2.5	2.5
4	<i>Megachile wheeleri</i> Mitchell ^b	20.0	0.8	22.0	9.2	9.2	10.6	10.2	13.3
5	<i>Osmia intergra</i> Cresson ^b	0	0	0.8	6.7	0.8	2.0	2.1	2.8
Plants									
6	<i>Abronia latifolia</i> Eschscholtz	0	0	0	6.7	9.2	3.8	4.0	5.3
7	<i>Achillea borealis</i> Bongard	0	0	0.8	13.0	1.7	3.8	4.0	5.3
8	<i>Aira praecox</i> L. and <i>A. caryophyllea</i> L.	0	12.5	35.0	14.0	25.0	20.8	21.7	24.7
9	<i>Arctostaphylos uva-ursi</i> (L.) Sprengel	0	0	0.8	0	4.2	1.2	1.3	1.7
10	<i>Artemisia pyconocephala</i> DC.	0	0	0.8	0	0.8	0.4	0.4	0.6
11	<i>Avena</i> sp.	20.0	0	0	0	0.8	1.0	0.2	0.3
12	<i>Oenothera cheiranthifolia</i> (Sprengel) Raim	0	0.8	13.0	15.0	8.3	8.8	9.2	11.9
13	<i>Carex obnupta</i> L. Bailey	0	85.0	5.0	0	0	21.6	22.5	1.7
14	<i>Erigeron glaucus</i> J. Belenden	0	0	0.8	33.0	4.2	9.2	9.6	12.8
15	<i>Eriogonum latifolium</i> Smith	0	0	5.8	38.0	31.0	18.0	18.8	25.0
16	<i>Festuca</i> sp.	70.0	0.8	0	0	3.3	3.8	1.0	1.1
17	<i>Fragaria chiloensis</i> Duchesne	20.0	5.8	22.0	24.0	28.0	20.0	20.0	24.7
18	<i>Gaultheria shallon</i> Pursh	0	0.8	0	0	0	0.2	0.2	0
19	<i>Gnaphalium</i> sp.	0	5.8	11.0	6.7	15.0	9.2	9.6	10.8
20	<i>Hypochoeris radicata</i> L.	0	19.2	23.0	2.5	8.3	12.6	13.1	11.1
21	<i>Juncus falcatus</i> E. Meyer	0	16.7	5.8	0	0	5.4	5.6	1.9
22	<i>Juncus lesueurii</i> Bolander	0	65.8	94.0	5.0	9.2	41.8	43.5	36.1
23	<i>Lathyrus littoralis</i> (Nuttall) Endlicher	0	0	5.8	50.0	17.0	17.4	18.1	24.2
24	Lichen	10.0	0.8	4.2	0	0	1.6	1.3	1.4
25	Lichen & Moss	0	0	10.0	0	0	2.4	2.5	3.3
26	<i>Lotus micranthus</i> Bentham	10.0	5.8	1.7	0	6.7	3.8	3.5	2.8
27	<i>Lotus purshianus</i> (Bentham) F. E. & E. G. Clements	0	24.2	11.0	0	3.3	9.2	9.6	4.7

Table 2. Continued.

#	Species	Percent of sample units							
		A Pasture	B Lowland	C Transition	D Foredune	E Inland	ABCDE	BCDE	CDE
28	<i>Carpobrotus chilense</i> (Molina) N. E. Brown.	0	0	2.5	18.0	0	4.8	5.0	6.7
29	Moss	30.0	44.2	5.0	14.0	25.0	22.4	22.1	14.7
30	<i>Castilleja exserta</i> (A. A. Heller) Chuang & Heckard	0	0	0	13.0	2.5	3.8	4.0	5.3
31	<i>Parenthuchellia viscosa</i> (L.) Caruel	0	3.3	0	0	0	0.8	0.8	0
32	<i>Poa douglasii</i> Nees	0	0	6.7	32.0	37.0	18.0	18.8	25.0
33	<i>Polygonum paronychia</i> Chamisso & Schlechtendal	0	0	0	0	1.7	0.4	0.4	0.6
34	<i>Potentilla anserina</i> L. ssp. <i>pacifica</i> (Howell) Rousi	0	13.3	0.8	0	0	3.4	3.5	0.3
35	<i>Pteridium aquilinum</i> (L.) Kuhn	0	0	0	0	2.5	0.6	0.6	0.8
36	<i>Salix</i> sp.	0	11.7	0	0	0	2.8	2.9	0
37	<i>Solidago spathulata</i> DC.	60.0	1.7	33.0	8.3	40.0	22.4	20.8	27.2
38	<i>Trifolium microcephalum</i> Pursh	0	0	0	0	18.0	4.2	4.4	5.8
	<i>n</i> =	20	120	120	120	120	500	480	360

^a Hymenoptera: Sphecidae.^b Hymenoptera: Megachilidae.

Table 3. Significant associations between *Megachile wheeleri* nests (Sp. A) and other species (Sp. B). Determined by pairwise contingency table comparisons.

Sp. B	# Sample units with species				Statistical tests ^a		Association index				Type
	Both	Sp. A	Sp. B	Neither	χ ²	P	Jaccard	Dice	Ochai	Yule	
Lowlands, Transitional Dunes, Foredunes, and Inland Dunes combined (<i>n</i> = 480)											
VR = 1.42, Association Index for the 6 positively associated species ^b , Test Statistic W = 681.90, <i>P</i> < 0.005											
<i>Aira</i> ^c	23	15	79	363	35.535	0.0001	0.20	0.33	0.37	0.28	+
<i>Juncus lesueurii</i>	23	15	186	256	4.121	0.0423	0.10	0.19	0.26	0.10	+
Moss	16	22	90	352	8.392	0.0038	0.13	0.22	0.25	0.14	+
<i>Solidago</i>	14	24	86	356	5.402	0.0201	0.11	0.20	0.23	0.12	+
<i>Ammophila azteca</i>	5	33	14	428	6.747	0.0094	0.10	0.18	0.19	0.14	+
<i>Carex</i>	2	36	106	336	5.999	0.0143	0.01	0.03	0.03	0.12	—
<i>Lathyrus</i>	1	37	86	356	5.59	0.0181	0.01	0.02	0.02	0.12	—
Transitional Dunes (<i>n</i> = 120)											
<i>Ammophila azteca</i>	6	14	8	92	5.838	0.0157	0.21	0.35	0.36	0.26	+
Foredunes (<i>n</i> = 120)											
<i>Aira</i> ^c	6	2	11	101	21.001	0.0001	0.32	0.48	0.51	0.47	+
Moss	4	4	13	99	6.169	0.0130	0.19	0.32	0.34	0.27	+
Inland Dunes (<i>n</i> = 120)											
<i>Aira</i> ^c	6	3	24	87	6.767	0.0093	0.18	0.31	0.37	0.27	+
<i>Gnaphalium</i>	4	5	14	97	4.355	0.0369	0.17	0.30	0.31	0.23	+

^a Continuity corrected for df = 1; No cells with expected frequency < 1, no 2 cells < 5.
^b Multispecies association test of *M. wheeleri* nests and 6 positively associated species (Schluter (1984), Ludwig & Reynolds 1988). Negative associations were not significant.
^c *Aira praecox* and/or *Aira caryophylla*.

120 = 0.62) contained significantly more nests per SU than the other two strata pooled together (122/240 = 0.51) (*U* = 13047, *P* = 0.006, *n*₁ = 240, *n*₂ = 120) (Mann-Whitney *U*-test). The significant difference resulted even though the total number of nests within the Foredunes exceeded the number of nests within Transitional Dunes (Table 4). This is because most SUs in all three strata contained less than five nests, with two or three containing up to twenty nests, but Foredunes had one SU containing 42 nests. Twice as many Transitional Dunes SUs contained nests than either the Foredunes or Inland Dunes.

Although nests of *Anthidium palliventre* Cresson and *Osmia integra* Cresson were found in the same nest habitats as *M. wheeleri*, neither were sufficiently abundant to detect statistically significant associations with plants. A significant association was detected between the sphecid wasp *Ammophila azteca* Cameron and the nests of *M. wheeleri* (Table 3). The sphecid *Bembix americana comata* J. Parker was previously known to nest in dense aggregations in barren sand in the preserve (Gordon 1984), but single nests were found in SUs in other habitats (Tables 2 and 4).

Associations.—None of the SUs contained the introduced plants *L. arboreus* or *A. arenaria*. Pairwise contingency table analyses revealed significant positive associations between *M. wheeleri* nests and *Aira*, *S. spathulata*, *J. lesueurii*, and moss (Table 3). All four species were present in more than 20% of the SUs, many of which did not contain *M. wheeleri* nests (Tables 2 and 3). *Aira* co-occurred with nests in a higher proportion (19%) of the SUs containing nests than *J. le-*

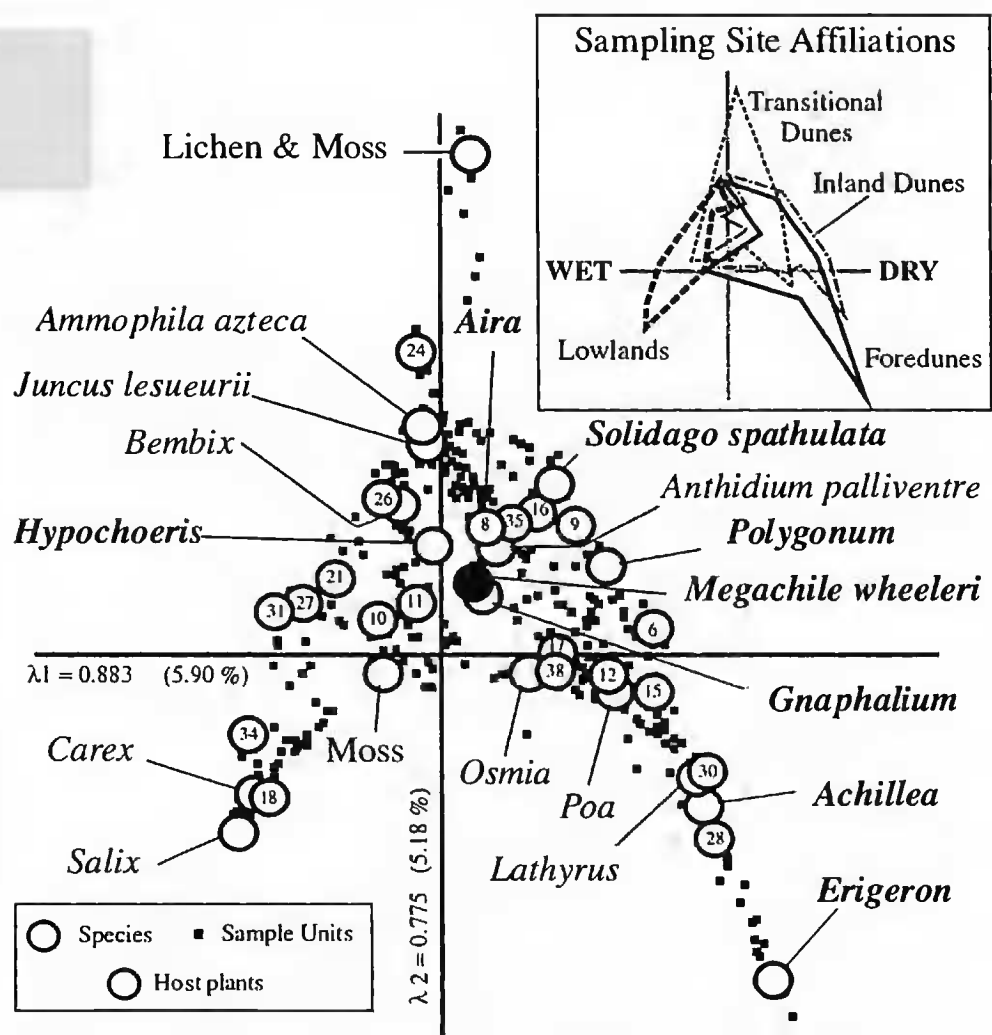


Figure 1. Correspondence analysis of bee and wasp nests, plant species, and sample units. The distance between *M. wheeleri* nests and *Solidago* is not based on the association between the two alone, but reflects the relationships among all species and sample units simultaneously. Refer to Table 1 to identify species numbers. Boundaries of strata from which sample units were drawn are indicated within inset.

sueurii, *Solidago*, or moss (10, 11 and 13% respectively, Table 3). In other words, all four plant species were common in all four habitats, but *Aira* and nests co-occurred in a more SUs than the other three plants. With the exception of *Solidago*, nests were not constructed in the immediate proximity of the plants the bee forages on. Significant negative associations occurred between nests and *Carex obnupta* L. Bailey and *Lathyrus littoralis* (Nuttall) Endlicher. The variance test

Table 4. Proportions of bee and wasp nests recovered in each habitat.

Species	Proportion of total nests for each species						Total # nests
	A Old pasture	B Lowland	C Transi- tional	D Foredune	E Inland	CDE Combined	
Megachilidae							
<i>Megachile wheeleri</i>	0.030	0.005	0.365	0.414	0.187	0.966	203
<i>Anthidium palliventre</i>	0	0.077	0.231	0	0.692	0.923	13
<i>Osmia integra</i>	0	0	0.023	0.932	0.045	1.0	44
Sphecidae							
<i>Bembix americana comata</i>	0.1	0.150	0.500	0	0.250	0.750	20
<i>Ammophila azteca</i>	0	0.065	0.806	0.032	0.097	0.935	31
<i>n</i> =	20	120	120	120	120	360	500

Table 5. Habitat utilization for nesting by *Megachile wheeleri*. Numbers of sample units containing nests in each habitat, and results of contingency table tests comparing habitats.

	Inland dunes	Foredunes	Transitional	Lowlands	
Present	9	20	5	1	
Absent	111	100	115	119	
Contingency table tests			χ^2	$P =$	
Inland	Foredunes		0.683	0.4087	
Inland	Foredunes	Transitional	11.757	0.0028	
Inland	Foredunes		Lowland	6.678	0.0355

(Schluter 1984) was highly significant for all positively associated species, but not significant for the two negatively associated species. There was no significant correlation between total plant cover and numbers of *M. wheeleri* nests ($r = 0.019$, $n = 484$).

The first five axes of correspondence analysis explained 24.96% of the variance. The results from analyzing 464 SUs (Table 2) are presented in Fig. 1. The Inland Dunes and Foredunes SUs overlap, but were distinctly different from the Lowlands. Transitional Dunes overlapped with all three other strata but also contained a number of unique sample units. Sample units containing *M. wheeleri* nests occurred within the region of overlap among Transitional Dunes, Foredunes and Inland Dunes (Fig. 1). *Gnaphalium* sp. was the plant species most closely associated with *M. wheeleri*. *Salix* sp., *Carex obnupta*, *Erigeron*, and Lichen-Moss displayed negative associations with *M. wheeleri*. Comparing host plants with nests, there were closer associations with *Solidago* and *Hypochoeris* than with *Achillea* or *Erigeron*.

Except for *Gnaphalium* and *Hypochoeris*, the other species clustering near *M. wheeleri* nests in Fig. 1 were all rare (Table 2), so pairwise associations with nests were not significant. Although *Gnaphalium* and *Hypochoeris* distributions across strata were similar to that for *M. wheeleri* nests, both plants had substantial presence in the Lowlands, where nests did not occur, so they did not co-occur with nests in enough SUs for significant pairwise associations. Within Inland Dunes a significant association was detected with *Gnaphalium* (Table 3).

DISCUSSION

Nest Distribution.—Since *M. wheeleri* was the only leafcutter known to use goldenrod leaves, it was concluded that species occupied the trap nests. The low occupancy rate of buried and surface trap nests, the fact that none of the trap nests in trees were occupied, and the high mortality within trap nests placed in dense nest aggregations support the assertion that *M. wheeleri* is a ground-nesting species. However, some individuals did take advantage of pre-existing holes.

Megachile wheeleri nests were restricted to “*Poa-Lathyrus*” community type within the “natural” dunes system, but did occur in some disturbed sites, as evidenced by nests found in the Old Pasture. Transitional Dunes appeared to be preferred over Inland Dunes and Foredunes, as evidenced by higher brood cell concentrations within SUs and the significantly higher proportion of SUs occupied (Tables 2 and 4).

The Lowlands often contain vernal ponds for several months (Wiedemann 1984, Gordon 1992a), which could create high mortality from drowning. Therefore it was not surprising that bees and wasps do not nest there. However, *M. wheeleri* constructed dense nest aggregations in the Transitional Dunes a few centimeters away, suggesting that Lowlands can be discriminated in some way during the dry season. Since there was no correlation between nest density and plant cover, plant density is probably not the primary cue. There often was no apparent difference between Transitional Dunes and Lowlands other than elevation and plant species composition, so it is not clear what cues bees may use. Perhaps residues left by microorganism blooms in the vernal ponds cement sand particles more tightly or moisture or chemicals are avoided. It has been shown that the root microflora associated with *Carex* influences the plant community composition in similar habitats (Chapman 1976), so it is possible that chemical cues are involved.

Associations.—Some combination of *Solidago*, *J. lesueurii*, *Aira* or moss within a specific site would be a good indication that *M. wheeleri* nests may be found there. While collecting hundreds of brood cells needed for concurrent projects, it became evident that *Aira* alone was a good indicator of nesting sites. Even though *Aira* patches did not always contain nests, they were reliable sources. Overall, *Aira* is the single best indicator plant for potential *M. wheeleri* nest habitat, and the presence of *Solidago*, *J. lesueurii* or moss strengthens the prediction.

Nests in Fig. 1 are more closely associated with *Gnaphalium* and several other species than with *Juncus* or *Solidago*. Although this appears to conflict with results from contingency tables, it does not. Correspondence analysis describes the relationships between all species and SUs simultaneously, not individual associations between species pairs. Figure 1 provides a description of plant associations that is consistent with personal experience and previous classifications (Wiedemann et al. 1974, Wiedemann 1984, Barbour & Johnson 1988) even though the SU size is small for a plant community study.

Soil texture appears to be a major factor determining suitability of nest sites and nesting will occur in association with a number of plant species which aggregate sand. Such shallow nests constructed in loose sand would probably collapse and contaminate the nest provision. Most nests were constructed within the dense, fibrous root systems of grasses which bound the sand. The few nests found in the Old Pasture were also associated with other species of grasses, as were nests excavated in other sites off the preserve for a concurrent study. Nests beneath moss in the Foredunes and Inland Dunes were also in well aggregated sand.

Relationships to Plant Community Change.—Natural plant succession and the encroachment of introduced plants are both expected to effect nesting habitat, nest distribution and abundance of *M. wheeleri*. Over a ten year period nest habitat has been expanding as Transitional Dunes habitat has been developing where barren sand in the deflation plain has been invaded by early successional vegetation (personal observation). This newly developed habitat was being colonized by *M. wheeleri*, and nest density should be expected to increase there in the future. Because of the potential area involved, considerable additional habitat suitable for nesting should continue to develop within the preserve. In the long term, as forested hollows develop and progress to the climax community, *M. wheeleri* nest habitat and foraging resources should be eliminated. Therefore, long term survival

of *M. wheeleri* populations within the L-CDP will probably depend on maintenance of Foredune, Inland Dune and Transitional dunes habitats through disturbance of the developing forest.

The *Poa-Lathyrus* plant community reflects the natural nesting habitat for *M. wheeleri* in these coastal dunes. The encroachment of introduced plants such as bush lupine (*L. arboreus*) (Miller 1988) or European beach grass (*A. arenaria*) (Wiedemann 1984) is expected to reduce *M. wheeleri* numbers by displacing nesting habitat and host plants. Within habitats that are dominated by these non-native species, *M. wheeleri* nests did occur within refugia of native plants, mosses and other introduced grasses (Gordon 1992a), but the impact of the encroachment of bush lupine and European beach grass on the overall *M. wheeleri* population was not examined.

Although some introduced plants (*L. arboreus*, *A. arenaria*) may reduce nesting habitat, it is interesting to speculate that others may increase it. *Megachile wheeleri* nests were most commonly found among *Aira praecox* and *A. caryophyllea* which are introduced species (Hickman 1993). This raises interesting questions regarding potential beneficial interactions between *M. wheeleri* and *Aira* in the dunes. Plant growth in coastal dunes is limited by deficiencies of essential nutrients (reviewed in Chapman 1976, Barbour et al. 1985) because they are readily leached away from the sand (Carter 1988). The leaf cuttings, cocoons, pollen and feces from *M. wheeleri* nests should increase the amount of nutrients available and the sand's ability to retain water. Cocoons which had passed the winter in the sand were completely engulfed by roots with little trace of leaves or feces remaining. By nesting in *Aira*, *M. wheeleri* may enhance growth of the grass within the site and, as a result, the grass's expanding root system may provide more nesting habitat for bees by improving soil structure.

Defining Bee Nesting Habitat.—This study demonstrated that plant associations can be used to characterize nest sites of *M. wheeleri* within the L-CDP, and probably other bees and wasps as well. However, *M. wheeleri* has a broad distribution and different plant species associations probably characterize nest habitats in different locations. In fact, it appears that *M. wheeleri* nest sites in disturbed habitats near the study site are characterized by other plants. The abundance of *M. wheeleri* within the preserve allowed detection of significant associations with plants. However, very large sample sizes may be required to detect significant associations for bee or wasp species that are not abundant or have widely dispersed nests.

This study also demonstrated that *M. wheeleri* exhibited variation in nesting behavior ranging from dense aggregations to scattered individual nests, and that other hymenoptera species also nest within those aggregations. Individual nests of the sphecoid wasp *Bembix americana comata* were detected in vegetated habitats in this study (Table 2), including within *M. wheeleri* nest aggregations. *Bembix americana comata* primarily nested in dense aggregations in open below sand on the preserve (Gordon 1984) and wide variation in nesting habitat was also demonstrated for that species by this study.

Conserving Native Bees.—There is a growing awareness of the need to protect pollinators of native plants (Tepedino 1979, LaSalle & Gauld 1993, Buchmann & Nabhan 1996). Long term success in restoring (Miller et al. 1992) or maintaining diverse native plant communities may also depend on successful re-estab-

lishment and maintenance of pollinator communities (Thorp 1990). This study suggests that *M. wheeleri* contributes soil nutrients within these sandy nesting habitats by transferring pollen and leaf material from its host plants into the ground. This role of native bees, which has not been fully appreciated by conservationists, provokes some interesting questions regarding the potential interdependence of the structures of bee and plant communities.

ACKNOWLEDGMENT

The Nature Conservancy's Lanphere-Christensen Dunes Preserve and the Humboldt State University L-CDP Research Advisory Committee granted permission to work on the preserve. Preserve managers Andrea Pickart and Linda Miller provided useful information and references from the preserve library. Ted Kuiper and I. D. Christensen provided supplies and facilities, and I. D. Christensen provided housing at the study site. Tom Duebendorfer identified several plant species and discussed plant associations. Marcel Rejmanek provided computer programs and useful suggestions regarding analyses. Robbin Thorp, James Carey, Christine Peng, John Barthell, Ken Lorenzen, and an anonymous reviewer provided useful comments on the manuscript. Submitted in partial fulfillment of the requirements of the Ph.D. at the University of California, Davis.

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Received 23 Jan 1997; Accepted 6 Jul 2000.